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Predicted extinction of unique genetic diversity in marine forests of *Cystoseira* spp.

Roberto Buonomo[a,b,*], Rosa M. Chefaoui[b], Ricardo Bermejo Lacida[c,d], Aschwin H. Engelen[b], Ester A. Serrão[b,1], Laura Airoldi[a,1]

[a] Dipartimento di Scienze Biologiche, Geologiche ed Ambientali, University of Bologna, UO Conisma, Via S. Alberto 163, 48123, Ravenna, Italy
[b] CCMAR-CIMAR Centre of Marine Sciences, Universidade do Algarve, Faro, Portugal
[c] Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, Spain
[d] Irish Seaweed Research Group & Earth and Ocean Sciences Department, Ryan Institute and School of Natural Sciences, National University of Ireland, Galway, Ireland

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ABSTRACT

Climate change is inducing shifts in species ranges across the globe. These can affect the genetic pools of species, including loss of genetic variability and evolutionary potential. In particular, geographically enclosed ecosystems, like the Mediterranean Sea, have a higher risk of suffering species loss and genetic erosion due to barriers to further range shifts and to dispersal. In this study, we address these questions for three habitat-forming seaweed species, *Cystoseira tamariscifolia*, *C. amentacea* and *C. compressa,* throughout their entire ranges in the Atlantic and Mediterranean regions. We aim to 1) describe their population genetic structure and diversity, 2) model the present and predict the future distribution and 3) assess the consequences of predicted future range shifts for their population genetic structure, according to two contrasting future climate change scenarios. A net loss of suitable areas was predicted in both climatic scenarios across the range of distribution of the three species. This loss was particularly severe for *C. amentacea* in the Mediterranean Sea (less 90% in the most extreme climatic scenario), suggesting that the species could become potentially at extinction risk. For all species, genetic data showed very differentiated populations, indicating low inter-population connectivity, and high and distinct genetic diversity in areas that were predicted to become lost, causing erosion of unique evolutionary lineages. Our results indicated that the Mediterranean Sea is the most threatened region, where future suitable *Cystoseira* habitats will become more limited. This is likely to have wider ecosystem impacts as there is a lack of species with the same ecological niche and functional role in the Mediterranean. The projected accelerated loss of already fragmented and disturbed populations and the long-term genetic effects highlight the urge for local scale management strategies that sustain the capacity of these habitat-forming species to persist despite climatic impacts while waiting for global emission reductions.

1. Introduction

The distributions of species are predicted to become increasingly affected by climate warming (Sunday et al., 2012). Geographic range shifts caused by recent temperature changes have been described for many marine species, including sessile ecosystem structuring canopies (e.g., Helmuth et al., 2006; Smale and Wernberg, 2013; Nicastro et al., 2013; Lourenço et al., 2016). In sessile species, range shifts happen by local extinction at the trailing edge and dispersal and colonization of new areas at the expanding edge. Species and entire communities can be locally lost as their latitudinal distribution limits move tracking the climatic niche (Wernberg et al., 2011). Range extension, on the other hand, can be limited by dispersal barriers and habitat availability preventing colonization of new areas and forcing species into progressively unsuitable climatic conditions. Similarly to mountain-top microclimate contraction, warming beyond available habitat can drive species to extinction (Wernberg et al., 2011). Furthermore, as the simultaneous shift of whole assemblages is unlikely (Hawkins et al., 2009), the resilience of communities and their ability to sustain ecosystem functioning and services in warming climate depends also on the availability of species able to occupy key functional roles left by displaced species (Pecl et al., 2017). Coastal ecosystems in geographically bounded regions and with high levels of endemism, such as islands and enclosed seas, are particularly exposed to extinction risks and erosion of

* Corresponding author. Dipartimento di Scienze Biologiche, Geologiche ed Ambientali, University of Bologna, UO Conisma, Via S. Alberto 163, 48123, Ravenna, Italy.
E-mail addresses: roberto.buonomo2@unibo.it (R. Buonomo), eserrao@ualg.pt (E.A. Serrão), laura.airoldi@unibo.it (L. Airoldi).
[1] Equal contributors.

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resilience from changing climatic conditions and other human impacts, because of limited habitat availability and barriers for new colonizations (Peters et al., 2015).

Distributional range shifts are a product of a complex interaction of factors: abiotic conditions, biotic interactions, dispersal potential and evolutionary capacity (Soberon, 2005), which complicate predictions of future distributions. However, mechanistic understanding of these processes at the community level is commonly limited, and alternative modelling approaches have been suggested based solely on climatic data (Bates et al., 2014), for which future predicted values are available and have successfully been applied in marine species (e.g., Assis et al., 2014, 2018; Neiva et al., 2015). The distribution ranges of marine species tend to follow their thermal limits closely and have been directly responsive to climate warming, therefore allowing for confident predictions of latitudinal range contractions and expansions (Sunday et al., 2012). Assuming that correlative species distribution modelling based on environmental data approximates the fundamental "climatic" niche of a species, predictive models based on climatic data may be suitable for large-scale range shift predictions (Peterson, 2006; Kearney and Porter, 2009).

When species are subject to rapid changes in their distribution, they can be exposed to genetic erosion and loss of genetic diversity (Hampe and Petit, 2005; Nicastro et al., 2013; Neiva et al., 2015). Such loss results from genetic drift and bottlenecks in small populations left behind at rear range edges and from founder effects at the expanding leading edge. There is growing interest in the genetic consequences of species distribution range shifts (Pfenninger et al., 2012), because of their implication for the future persistence of the species and the ecosystems they support (O'Leary et al., 2017). Loss of genetic variability can result in loss of adaptive potential and resilience to unfavourable environmental conditions (e.g., Pearson et al., 2009). This is especially the case for species with geographically skewed distributions of genetic diversity (Neiva et al., 2014; Assis et al., 2016b), where populations suffer different levels of demographic oscillations across their range. Species with longer generation times, limited population connectivity, and restricted dispersal are more prone to local extinction and genetic erosion due to changes in climate conditions (Bates et al., 2014). Key foundation marine species that fit these criteria include canopy-forming brown algae.

Kelp and fucoid canopy algae form some of the most productive, diverse and valuable marine habitats, creating dense three-dimensional structures supporting high biodiversity (Benedetti-Cecchi et al., 2001; Steneck et al., 2002; Voerman et al., 2013), and providing essential ecosystem services (Cheminée et al., 2013; Mineur et al., 2015). These species are typically characterised by short propagule dispersal, making propagule availability an important limitation to the establishment of new populations and restricting gene flow (e.g., Engelen et al., 2008; Buonomo et al., 2017). This, together with their sensitivity to a variety of stressors, makes these species particularly vulnerable (Sales et al., 2011; Strain et al., 2014; Mineur et al., 2015). Declines of canopy habitats have been reported worldwide, driven by multiple anthropogenic impacts (Verges et al., 2014, Vergés et al., 2016; Coleman et al., 2008; Connell et al., 2008; Mangialajo et al., 2008; Airoldi et al., 2015), and climatic factors are accelerating their loss at the range edges (Perkol-Finkel and Airdoli, 2010; Araújo et al., 2016; Wernberg et al., 2016; Assis et al., 2018). Such rapid range contractions could trigger the loss of genetic diversity because of low dispersal rates (Assis et al., 2017; Buonomo et al., 2017), further decreasing population resilience (Wernberg et al., 2018). Indeed, local to regional extinctions are increasingly reported at range edges, namely for fucoid algae (Smale and Wernberg, 2013; Nicastro et al., 2013; Assis et al., 2014; Neiva et al., 2015; Lourenço et al., 2016; Thibaut et al., 2016) and kelp (Martinez et al., 2003; Assis et al., 2013; Fernández, 2016). Climate change-driven local extinction and range shifts may cascade down on the associated ecosystems, changing community diversity and interactions, and key functions and services (Smale et al., 2013; Bracken et al., 2007). Despite all this evidence for climatic effects on ecosystem-structuring populations at range edges, their consequences for gene pools and evolutionary potential are insufficiently understood, but likely to be of major significance because many range edges contain differentiated populations with high and unique genetic diversity (e.g., Diekmann and Serrao, 2012; Neiva et al., 2015). Genetic variability is mostly cryptic, not evident in the phenotypes, leading to undetected unreported shifts in genetic baselines as range shifts proceed (Assis et al., 2013, 2018).

Here we investigate the potential effects of climate change on species ranges and their genetic pools using various fucoid algae belonging to the genus *Cystoseira*. These are among the most important habitat-forming species in the Mediterranean and adjacent North Atlantic coasts and are suffering a marked decline (Thibaut et al., 2005; Serio et al., 2006). This is particularly concerning as many species of *Cystoseira* are endemic to this region, have rather restricted habitat distributions and have protected status (Annex II of the Barcelona Convention, COM/2009/0585 FIN; and 'Convention on the conservation of European wildlife and natural habitats'). We used three closely related species of *Cystoseira*, with distinct distribution ranges, specifically *C. tamariscifolia* (mostly Atlantic), *C. amentacea* (Mediterranean) and *C. compressa* (both Atlantic and Mediterranean) to 1) estimate the spatial distribution of population genetic diversity and differentiation throughout their entire distributions in the Atlantic and Mediterranean, 2) model their present and predict their future ranges according to different climatic scenarios and 3) assess the consequences of predicted range shifts for their gene pools. This comparative approach allowed us to infer future conservation challenges for key structural species of the Mediterranean and Atlantic and highlighted particularly high threat levels for Mediterranean endemic biodiversity.

2. Methods

2.1. Biological data and study area

Cystoseira is a widely distributed genus of brown algae of the Fucales order and is found mostly in temperate regions of the northern hemisphere. It currently comprises at least 42 species (Algaebase - Guiry and Guiry, 2013) a majority of which is endemic of the Mediterranean or Atlantic-Mediterranean regions (e.g., Taşkin et al., 2012). The species *C. tamariscifolia* occurs exclusively in the Atlantic and the entrance to the Mediterranean, *C. amentacea* is a Mediterranean endemic, and *C. compressa* occurs throughout the Mediterranean but also in the Atlantic transition zone (Iberia and NW Africa) and the Azores islands. We compiled georeferenced presence records from our field observations conducted as we sampled populations throughout their distributions for genetic analyses (see below), and from available literature and online databases. We found 54 publications (Table S1) with a useful description of species location and used two available databases: Algaebase (Guiry and Guiry, 2013) and the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/). All the records were double-checked and corrected for referencing errors and misplacement. We used a resolution of 5 arc minutes (~9.2 km) for georeferencing species data as well as the climatic variables. We obtained 265 occurrence records for *C. amentacea* (177 cells), 480 for *C. compressa* (287 cells), and 580 for *C. tamariscifolia* (315 cells). The study area covered the geographic distribution of the three species, comprising the Mediterranean and the Black Sea and the East coast of the North Atlantic Ocean, from Cape Verde islands to the Baltic Sea. As these species occur in shallow subtidal or intertidal zones, we delimited a 20 m depth threshold along the coastline from the 30 arc-seconds resolution GEBCO's gridded bathymetric dataset (http://www.gebco.net/).

2.2. Environmental data

We selected the most relevant ocean variables, available for both

current and future climatic conditions, according to previous literature on niche models of brown algae (Assis et al., 2014, 2016a, b; Neiva et al., 2014, 2015). Maximum, mean, minimum and range values of sea surface temperature (SST), surface air temperature (SAT) (because the upper limits of the species are in the intertidal zone), and mean salinity (particularly relevant in the Baltic) were used. For the present, data were obtained from Bio-ORACLE dataset (Tyberghein et al., 2012) and tested by Pearson's correlation coefficient < |0.7| in our study area. For the future, we produced a multi-model ensemble using five Ocean General Circulation Models (CNRM-CM5, HadGEM2-ES, IPSL-CM5A-LR, MPI-ESM-MR and NASA/GISS) pertaining to the Coupled Model Intercomparison Project Phase 5 (CMIP5; http://cmip-pcmdi.llnl.gov/cmip5/). We averaged 20 years of monthly data for 2050 (from 2030 to 2050) and 2100 (from 2080 to 2100) pertaining to two contrasting future scenarios: the high (RCP 8.5) and low (RCP 2.6) emissions scenarios of the IPCC Representative Concentration Pathways projections (Moss et al., 2010; van Vuuren et al., 2011). These scenarios allow projecting future environmental data according to different trajectories of socio-economic development and associated greenhouse gas emissions (van Vuuren et al., 2011).

2.3. Current and future SDMs

We implemented an ensemble approach to obtain the predictions for current distribution and the two future climate scenarios for the three *Cystoseira* species. We used the "biomod2" package (Thuiller et al., 2014) to perform six presence-absence algorithms: flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS), and randomForest (RF). Since reliable absence data were not available, we used two sets of pseudo-absences extracted at random in a proportion of ten pseudo-absences per presence cell as previously done in Chefaoui and Lobo. (2008). and Chefaoui et al. (2016). We evaluated predictive models by means of a repeated random subsampling validation. Data (presences and pseudo-absences) were split at random into a calibration (70%) and a validation set (30%) in each of the 10 iterations performed for each model and set of pseudo-absences. Thus, 120 models were computed for each species (2 pseudo-absence sets x 6 modelling techniques x 10 iterations) using randomly split subsamples.

We evaluated model performance using the true skill statistic (TSS; Allouche et al., 2006), the area under the receiver operating characteristic (ROC) curve (AUC), and ROC-derived sensitivity (presences correctly predicted) and specificity (absences correctly predicted) measures (Fielding and Bell, 1997), with the threshold that optimized ROC and TSS scores (Thuiller et al., 2014). The consensus prediction under current conditions for each species was an ensemble computed through the average of binary predictions (committee averaging ensemble), an approach which obtained the best performance predicting other coastal species (Chefaoui et al., 2016). To produce the ensemble, we strictly used just the models with TSS > 0.7. Ensembles were projected to the RCP 2.6 and RCP 8.5 scenarios to obtain the predictions for the future distribution. To assess the uncertainty in future projections related to the different values of each variable between the training range and the novel scenarios we computed a clamping mask. We estimated the importance of each variable following a procedure similar to "randomForest" (Liaw and Wiener, 2002). The correlation between the full model and a model rearranged without one of the variables using three iterations was calculated to obtain an importance value from 0 to 1 (highest importance) (Thuiller et al., 2014). Analyses were performed in R (R Core Team, 2015) using the CCMAR computational cluster facility.

2.4. Genetic analyses

Samples were collected at sites distributed along the distribution of each species. In total 33 populations were included in the analyses: 13 of *C. tamariscifolia,* 12 of *C. amentacea* and 8 of *C. compressa*. Three populations identified as *C. amentacea* along the Catalan coasts were included even if traditionally *C. mediterranea* is considered vicariant of *C. amentacea* in this area. However, in order not to influence the SDM, these populations were not used as input of the model itself. Several coastlines were extensively searched, but few populations were found (this was the case along Atlantic Morocco). Where species were found, a sample of 30–50 individuals was collected haphazardly, mostly by snorkeling or at extreme low tides, during the spring/summer. In some sites, smaller samples were collected due to smaller population sizes at the sites. The northern African coast was undersampled due to difficulties for travelling there.

Genomic DNA was extracted following a CTAB protocol (Hoarau et al., 2007). For *C. amentacea* and *C. tamariscifolia*, a selection of 6 microsatellites (Ct 2.7, Ct2.8, Ct2.9, Ct3.3, Ct4.3, Ct4.4. Genbank accession numbers: KX351509 - KX351512, KX351514, KX351515) previously developed for *C. tamariscifolia* was used (Engelen et al., 2017). For *C. compressa*, 10 specifically developed microsatellite markers were used (Cc01, Cc02, Cc04, Cc06, Cc07, Cc05, Cc09, Cc14, Cc22, Cc24, Genbank accession numbers: KY820873 - KY820875, KY820877 - KY820881, KY820883, KY820884). Fragment lengths were measured on an ABI PRISM 3130 DNA analyzer (Applied Biosystems) with the LIZ 500 (GeneScan) standard at the CCMAR sequencing platform. Alleles were scored using the free software STRand (Toonen and Hughes, 2001) and further binned into size classes with the msatAllele R package (Alberto, 2013). Departures from Hardy-Weinberg equilibrium (null hypothesis H_0: $F_{IS} = 0$) were tested with permutations implemented in GENETIX (Belkhir et al., 1996–2004) and confidence intervals were estimated by bootstrapping (number of replicates = 1000) within the DiveRsity R package (Keenan et al., 2013). Allelic richness and confidence intervals were determined after 999 resampling in DiveRsity. The STRUCTURE software was used to infer population structure (Pritchard et al., 2000). This analysis was replicated ten times and the mean of the permuted Q-matrices across replicates was obtained in CLUMPP (Jakobsson and Rosenberg, 2007). The resulting output was plotted with DISTRUCT (Rosenberg, 2002; http://www.cmb.usc.edu/noahr/distruct.html).

3. Results

3.1. Species distribution models

After correlation analysis, three variables were used for the modelling approach: maximum SST, minimum SST and the range of SAT. Overall validation scores were high for the models of the three *Cystoseira* species (Table S2). GBM, RF, and GLM obtained more accurate results, though no model performed consistently better across all species. FDA and MARS models for *C. tamariscifolia* and GLM for *C. compressa* produced lower validation scores in TSS than the threshold (TSS < 0.7) and were excluded from the ensemble model. Overall, *Cystoseira amentacea* obtained the highest validation scores in the ensemble model (TSS = 0.809) compared to *C. tamariscifolia* and *C. compressa* (TSS = 0.781 and 0.771 respectively).

Variable importance scores revealed differences depending on the species, although the highest relevance was always achieved by SST (Fig. S1). Minimum SST was the variable with greatest relative importance for the models of two mainly Mediterranean species: *C. amentacea* and *C. compressa,* suggesting that the lower SST of the Atlantic waters adjacent to the Mediterranean might be limiting their current distribution. For the Atlantic species, *C. tamariscifolia*, maximum SST obtained the highest scores in the models.

Ensemble models for current conditions correctly matched the present known distribution of the three species (Fig. 1, Fig. S2). *C. compressa* showed the wider longitudinal range, encompassing the eastern Mediterranean Sea from Greece and Turkey to the Azores

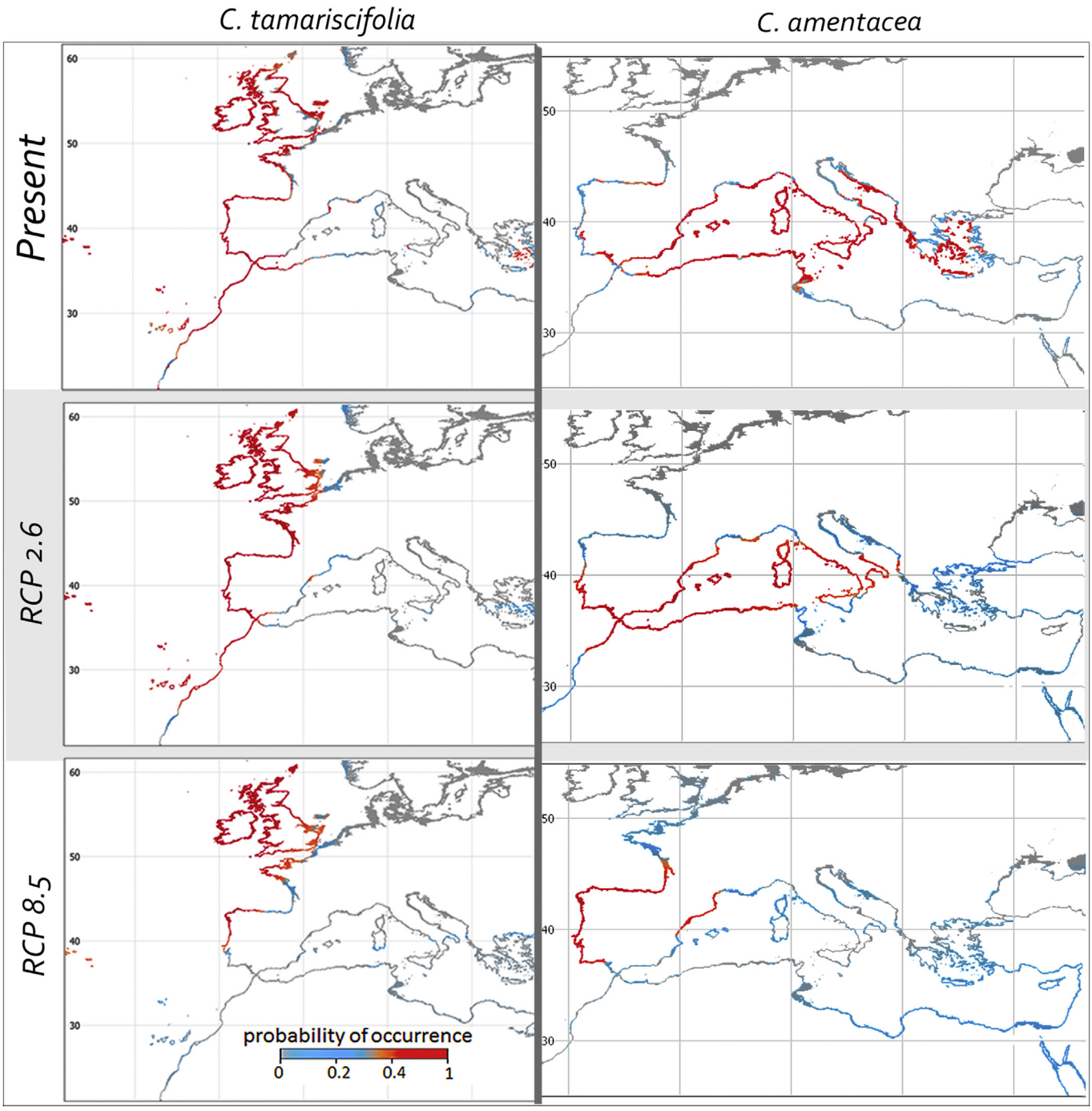

Fig. 1. Ensemble model maps showing the estimated probability of occurrence for *C. tamariscifolia* and *C. amentacea* for the present conditions and for the two contrasting future emission scenarios (least extreme RCP 2.6 and most extreme RCP 8.5) by 2100.

islands in the Atlantic Ocean. In the Atlantic coast, predictions for this species extended continuously from Morocco to the South of Portugal. Suitable climatic niche for the species was also found in the Cantabrian Sea, but we could not find records of *C. compressa* in this region, either because of discontinuity in the suitable habitat along the Portuguese coast or because of under-sampling efforts in the region. Suitable habitats for *C. tamariscifolia* are distributed mainly on the Atlantic coast, from the region of western Sahara to the North of England, with an intrusion in the Mediterranean coasts of southern Spain, Morocco and Algeria. According to its observed distribution and our models, *C. amentacea* is essentially a Mediterranean endemic species, with some potential suitable area in southern Portugal not supported by direct observational records, and low presence probability on the West coast of Portugal.

For 2050 our ensemble models predicted already considerable changes in probabilities of occurrence, particularly for the species *C. amentacea* and *C. compressa* (Fig. S3). For those species, only between 30% and 43% (depending on the RCP scenario) of the current distribution range was predicted to maintain a high probability of occurrence (Fig. 2). In contrast, in both scenarios, *C. tamariscifolia* showed much less loss of suitable area, conserving between 75% and the 81% of the present distributional area in the optimistic and pessimistic scenarios respectively. According to our model, by 2100, the present known distribution will largely retract due to a decrease in the

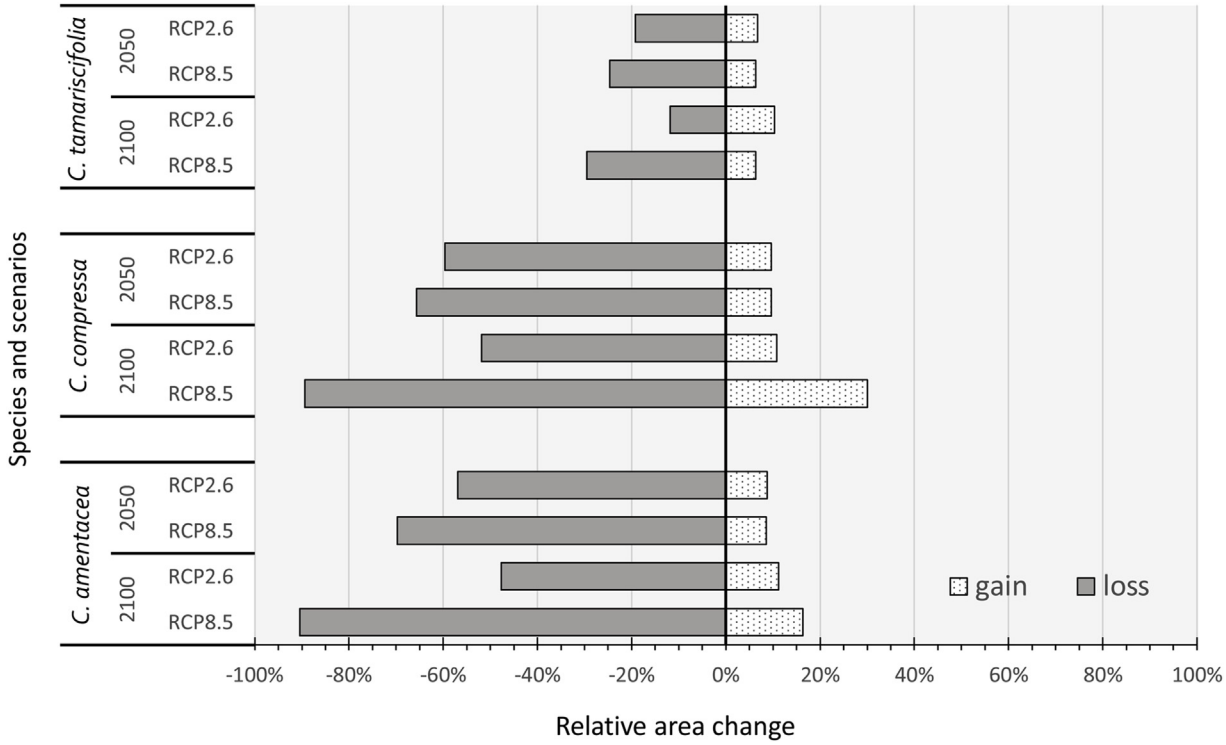

Fig. 2. Relative area change between the present and predictions under future climate scenarios (RCP 2.6 and 8.5) by 2050 and 2100 for the three *Cystoseira* species. Area is measured after reclassifying the models using a moderate probability of occurrence ($P > 0.3$). The largest loss is observed under RCP 8.5 scenario for the two species with Mediterranean distribution (*C. compressa* and *C. amentacea*).

probability of occurrence or loss of suitable area under both climate scenarios considered (Fig. 1, Fig. S2). However, some considerable differences could be found among species. For *C. compressa* the model predicted a 52% loss of original distributional area (medium to high suitable areas with probabilities of occurrence > 30%) in the optimistic scenario (Fig. 2). In the pessimistic scenario, a substantial increase of new suitable area was also predicted (30% of the original area of distribution), mostly along the Atlantic coasts of Portugal and France but the area lost in the Mediterranean Sea increased to 89%. The areas forecasted to become largely unsuitable for *C. compressa* are the central and eastern Mediterranean Sea ($P < 0.3$), especially Italian and Greek coasts where a large decrease in habitat suitability was predicted.

The ensemble model predicted a large range shift for *C. tamariscifolia* in the high emission scenario, in which the southern trailing edge would move about 2000 km north, from 20°N latitude to 33°N. However, this would not be compensated by an equal expansion of the leading edge further into the North Sea. The projected distributional range shift was much more conserved in the RCP 2.6 low emission scenario, in which the species would balance the net losses of suitable habitat with the expansion of new area (up to 10% of habitat with increased probability of occurrence, against a 12% decrease in area).

The suitable habitat for *C. amentacea* was predicted to contract considerably in the optimistic scenario and even more in the RCP 8.5 scenario, with habitat loss of 48% and 90% respectively. New suitable areas would only marginally compensate this habitat loss, as they accounted for only 11% in the optimistic and 16% in the pessimistic scenario. Furthermore, the overall probability of occurrence would be lower than current levels.

Uncertainty in future predictions using the RCP 8.5 scenario was higher than for RCP 2.6 in both 2050 and 2100 projections (Fig. S4). However, the areas with a higher uncertainty due to extreme values outside the range of the current conditions shared by both scenarios were limited to the Red Sea and some marginal areas of the Baltic Sea. Uncertainty areas were mostly limited to habitat with no presence or low probability of occurrence for all the species and did not affect the predictions substantially.

3.2. Population structure

The ten microsatellite markers used for *C. compressa* showed 3 to 19 alleles per locus (110 in total). Seven populations out of 8 exhibited a significant positive F_{IS} indicating heterozygote deficiency (Table 1). The average F_{ST} across all populations and loci was of 0.362. Higher genetic diversity was found in Iberian populations (Fig. S5) compared to Italian and French populations, with the latter showing the lowest allelic richness (Ar = 2.17) and gene diversity (H_E = 0.320). The best number of clusters (K = 8) matches the number of populations of *C. compressa* analyzed. Populations were differentiated, but some degree of admixture exists, particularly among the western Mediterranean populations.

C. amentacea exhibited highly variable markers with 15–33 alleles per locus. Half of the populations presented significant heterozygote deficiency. Population structure analysis found the best number of clusters at K = 10. Populations were highly differentiated across the basin (average F_{ST} = 0.510) and subdivision largely reflected geographic distance among populations. The Spanish population of Santa Pola was the only exception, which was assigned mainly to the same group of the population of Marseille (Fig. S6). When East (Italian) and West (France and Spain) Mediterranean populations were compared, eastern ones showed lower genetic diversity estimated as allelic richness (Ar), gene diversity (H_E) and number of private alleles (priv.all) (western: H_E: 0.77 ± 0.04, Ar: 16.50 ± 2.25, priv.all: 9.33; eastern H_E: 0.64 ± 0.12, Ar: 13.50 ± 2.88, priv.all: 6.33), however, these differences were non-significant.

C. tamariscifolia showed an average of 24 alleles/locus (13–42 alleles per locus) for six microsatellite markers. On average populations were highly differentiated (F_{ST} = 0.457) and genetic diversity, both estimated as allelic richness, as well as gene diversity (H_E) significantly

Table 1
Genetic diversity within sampling sites and geographical regions.

	Population	n	Ar	A′	He	Ho	F_{IS}	
C. tamariscifolia	**North**		**6.66**	**1.50**				
	Finavarra	29	1.18	0.00	0.02	0.02	−0.03	
	Polzeath	32	1.54	0.00	0.16	0.16	0.00	
	Roscoff	44	1.89	0.50	0.21	0.19	0.17	
	Noja	24	2.70	0.33	0.49	0.58	−0.18	
	Rieguabajo	32	2.89	0.17	0.37	0.36	0.03	
	Porcia	24	2.61	0.00	0.37	0.37	−0.05	
	Viana Do Castelo	47	1.75	0.17	0.20	0.14	0.32	
	South		**22.33**	**17.17**				
	Ericeira	24	5.22	1.67	0.60	0.57	0.03	
	Odeceixe	15	4.12	0.83	0.57	0.36	0.37	
	Sagres	31	7.44	4.00	0.70	0.73	−0.01	
	Albufeira	48	5.18	1.50	0.70	0.58	0.17	
	Tan-Tan	30	5.05	3.67	0.54	0.47	0.15	
	Tenerife	48	1.98	1.00	0.30	0.19	0.34	*
C. compressa	**West**		**8.30**	**4.10**				
	Albufeira	39	3.28	0.60	0.31	0.26	0.21	
	Murcia	38	3.93	0.80	0.42	0.33	0.41	*
	Mallorca	30	3.86	0.80	0.56	0.14	0.74	*
	Banyuls	35	2.18	0.40	0.32	0.00	0.99	*
	East		**6.90**	**2.70**				
	Sant'Elia	45	3.02	0.70	0.35	0.11	0.57	*
	Sciacca	26	2.99	0.90	0.41	0.10	0.68	*
	Porto Palo	28	2.73	0.30	0.39	0.32	0.37	*
	Montenegro	32	2.80	0.60	0.47	0.02	0.97	*
C. amentacea	**West**		**16.50**	**9.33**				
	Santa Pola	28	1.69	0.17	0.14	0.13	0.01	
	Tarragona	31	4.56	1.17	0.58	0.40	0.25	*
	Blanes	32	4.81	1.17	0.42	0.32	0.19	*
	Cap de Creus	28	4.93	2.00	0.57	0.34	0.43	*
	Mallorca	32	2.08	0.67	0.28	0.24	0.17	
	Marseille	30	3.87	2.17	0.42	0.38	0.06	
	East		**13.50**	**6.33**				
	Sant'Elia	30	4.57	1.67	0.52	0.45	0.14	
	Sciacca	25	3.12	0.50	0.31	0.24	0.33	
	Porto Palo	30	4.81	1.17	0.59	0.44	0.29	*
	Crotone	23	3.83	0.50	0.42	0.23	0.47	*
	Torre Uluzzo	25	1.98	0.33	0.17	0.15	0.05	
	Otranto	23	2.07	0.33	0.16	0.08	0.56	*

Ar: mean allelic richness per locus (999 resampling); A': mean number of private alleles per locus; He: Expected heterozygosity = gene diversity; Ho: observed heterozygosity; F_{IS}: multi-locus inbreeding coefficient (*if significant). In bold: populations grouping on geographic basis.

(Ar: $R^2 = 0.30$, $p = 0.05$; H_E: $R^2 = 0.37$, $p = 0.03$) decreased with increasing latitude (Fig. 3). A major genetic subdivision could be obtained already at K = 2, dividing the distribution into a northern and southern clade of 7 and 6 populations respectively. The highest levels of genetic diversity were found in the southern Portugal populations of Sagres and Albufeira. Northern populations showed much lower numbers of private alleles, allelic richness, and gene diversity when compared with the southern cluster.

4. Discussion

Our study revealed genetically distinct and low connected populations for all three species of *Cystoseira*. It also predicted extensive modifications of the distribution of suitable habitats with loss of genetic diversity in response to temperature changes, even in the best-case scenario of reduced greenhouse gases (GHG) concentration. The northern expansion of the distributional range, when possible along the Atlantic coasts, would only partially compensate for the loss of habitat at the southern distributional ranges, whereas the enclosed Mediterranean Sea would suffer considerable habitat retractions and erosion of unique evolutionary lineages.

4.1. Habitat loss at the trailing edges

Both scenarios used for the projections resulted in significant changes in predicted distribution of the species, and most of the habitat loss was observed already in the best-case scenario (RCP 2.6). Even in the low GHG simulation, important areas of the Mediterranean Sea would become partially or entirely unsuitable for *C. compressa* and *C. amentacea*. The Atlantic species, *C. tamariscifolia,* which could benefit from the availability of new favourable habitat further North, would be less affected by the best-case scenario but would still suffer heavy losses at its trailing edge in the worst-case scenario, with profound impact on the global gene pool of the species which is much richer at the southern range. This loss of suitable climatic conditions at the trailing edges is expected to drive local extinction, as local adaptation processes might hypothetically be restricted by intra-specific genetic diversity loss (e.g., Pearson et al., 2009; Hu and Fraser, 2016).

We found high and unique diversity in the regions most vulnerable to climate change according to the projections, especially in the case of *C. tamariscifolia* and partially for *C. amentacea.* High and unique diversity is harboured along the African coast and Gibraltar region. These probably acted as climatic refugia during the Last Glacial Maximum and as origin of secondary postglacial colonizations (Assis et al., 2014, 2016a,b; Lourenço et al., 2016). According to our model, this region corresponds to the expected trailing edge of the shifting distributional range for *C. tamariscifolia* and therefore has the highest probability to be lost in the future. The Mediterranean species showed a less clear gradient of diversity richness across the distribution range. However, every population of *C. amentacea* and *C. compressa* showed high level of distinctiveness, and the loss of any population would cause permanent loss of genetic variability from the genetic pool of the species (Hampe and Petit, 2005), which could hypothetically include locally adapted pools. Some admixture was found only for the more common species *C. compressa,* for which no strong West-East pattern of genetic diversity across the distribution could be found. Oceanic currents and habitat continuity play a significant role in dispersal and connectivity of some *Cystoseira* species (Buonomo et al., 2017). The greater connectivity of *C. compressa* inferred in our study could be explained by its buoyancy properties, which, in contrast with other *Cystoseira* species, has aerocysts on the apical branches, allowing for greater dispersal capability (Falace et al., 2005). Also, *C. compressa* is more tolerant to a variety of local anthropogenic stressors compared to other species of *Cystoseira* (Mangialajo et al., 2008) and has maintained a less fragmented presence across its range of distribution, which might have sustained a higher gene flow.

4.2. Colonization potential at the expanding edges

The predicted habitat shift of the expanding edge should allow for colonization of new areas, particularly along the North Atlantic and the North Sea coasts. *C. compressa* was predicted to thrive well mostly in its Atlantic distribution and extend further North like *C. tamariscifolia*. However, only for the latter species, the gained areas could quantitatively compensate the area lost at the trailing edge and only in the best-case scenario. Also, the actual spatial tracking of the environmental niche can lag behind the increase in suitable areas (Urban et al., 2012; Assis et al., 2017). Low dispersal traits can increase the time needed for effective colonization of new areas (Urban et al., 2012; Knutsen et al., 2013). This is especially the case if habitat is fragmented (Opdam and Wascher, 2004), and biotic interactions might limit settlement or development (Urban et al., 2012; Cahill et al., 2013). Geographic range expansions will occur starting from expanding marginal populations of the present distributional range that are, at least for *C. tamariscifolia,* already low in genetic diversity. This is the pattern expected and well documented for expansions into pre-glaciated regions (e.g., Neiva et al., 2012, 2014; Assis et al., 2016a). The expected range shift is likely to reduce further the heritable variability of marginal populations and

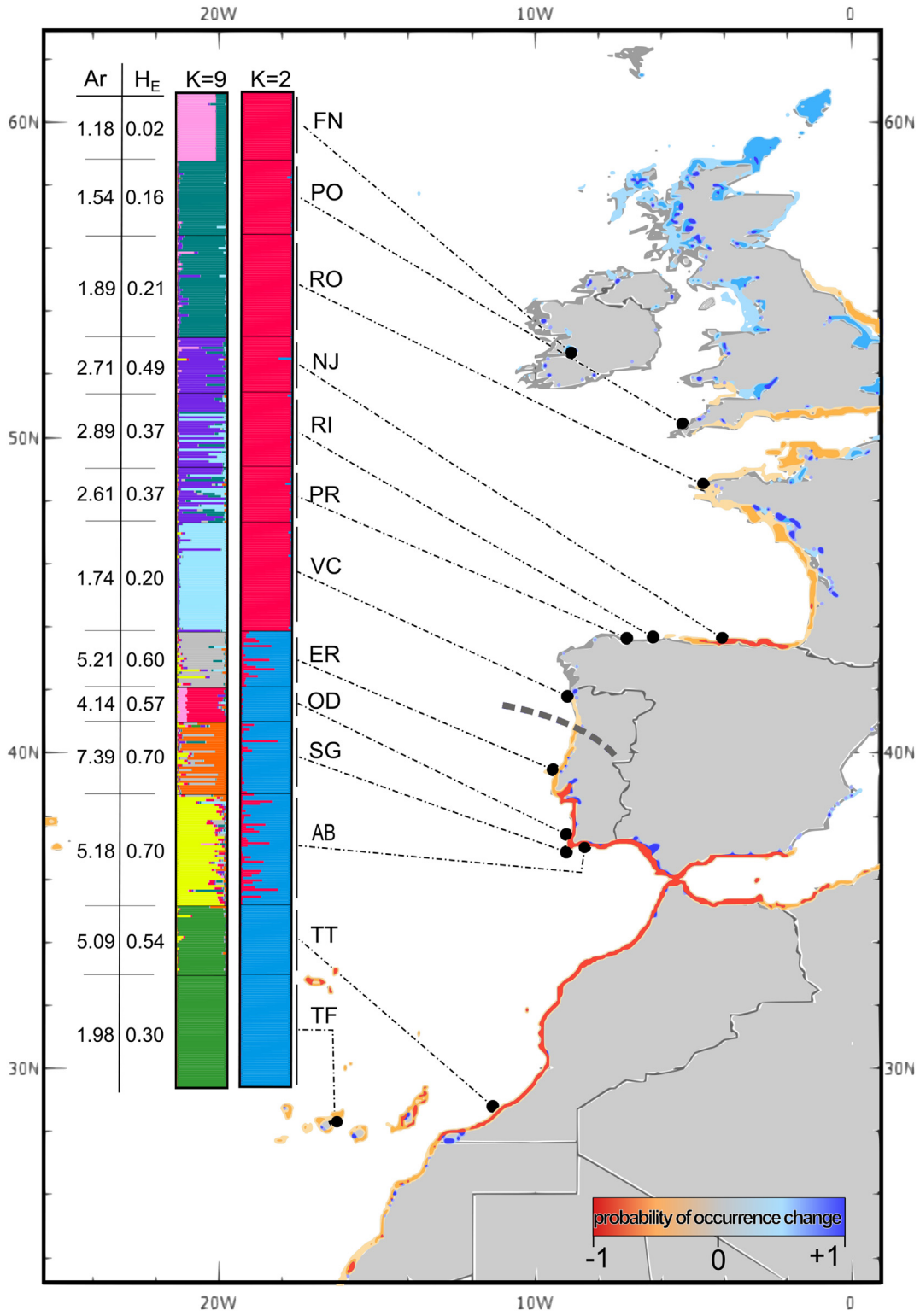

Fig. 3. *Cystoseira tamariscifolia* population genetic structure according to Structure analysis at the main subdivision (K = 2) and the subsequent structure (K = 9). Allelic richness (Ar) and gene diversity = expected heterozygosity (H_E) are indicated. Dotted line shows the main separation among north and southern lineages. Change in probability of occurrence between RCP8.5 at 2100 and present is also shown. Locations: Finavarra (FN); Polzeath (PO); Roscoff (RO); Noja (NJ); Rieguabajo (RI); Porcia (PR); Viana Do Castelo (VC); Ericeira (ER); Odeceixe (OD); Sagres (SG); Albufeira (AB); Tan-Tan (TT); Tenerife (TF).

compromise the ability to respond to selection under environmental changes (Pujol and Pannell, 2008). In contrast, the expanding edge for *C. compressa* would correspond to the Gibraltar Strait region, which does not present depleted genetic diversity compared to the genetic pool of the populations. Considering this species' higher dispersal capabilities, it might have better opportunities to succeed in colonizing new areas. *C. amentacea* was also predicted to find increasing suitable habitat towards the North Atlantic coasts. However, its fragmented distribution and lack of floating vesicles could drastically reduce the likelihood of dispersal (Buonomo et al., 2017), as demonstrated by low

levels of genetic exchanges among populations. Range shifts might also create new admixture zones at the Gibraltar Strait and adjacent Atlantic region, with possible hybridization particularly between *C. tamariscifolia* and *C. amentacea*. Hybridization between those species has been observed before, in contact zones (Gómez-Garreta et al., 1982; Amico et al., 1985), and could lead to unique combinations of private alleles and unexpected evolutionary consequences.

4.3. Mediterranean vs. Atlantic

As predicted, results confirm that the enclosed Mediterranean region will face substantially different ecological problems than the open North Atlantic coasts. According to our models, Atlantic populations of *Cystoseira* species will be subjected to significant changes in their distribution, but suitable climatic conditions will persist and eventually expand along most of the Atlantic range. Although the global area will not be as reduced as for the Mediterranean species, the evolutionary genetic consequences will be disproportionately large for the Atlantic species, because of the great impoverishment of the species gene pool as the southern populations become lost. This is due to the sharp gradient of variation of genetic diversity from South to North along the Atlantic coasts. This gradient spans a wide range of latitudes including previously glaciated areas which were likely to have been only recently colonized by the present populations, given their very low diversity and the unsuitable low sea surface temperatures of the recent last glacial maximum, ca. 20 Kyrs ago. From an ecological standpoint, the northwards expansion and colonization of new habitats by *Cystoseira tamariscifolia* in the Atlantic could result in unpredictable changes in ecosystems as the rocky shallow subtidal and intertidal shore is often shared with other canopy-forming species, such as *Laminaria* spp. and *Fucus* spp., which contribute to the structural complexity of the ecosystem and have a partially overlapping functional role (Airoldi and Beck, 2007).

In contrast with the Atlantic populations, Mediterranean ones are expected to suffer both major changes in climatic conditions and limited availability of new suitable habitats and possibilities for northern expansion. The Eastern Mediterranean is the region that will be most affected by the increase in SST, with strong effects on the habitat distribution of *C. compressa* and *C. amentacea*, already under the best-case scenario. Overall, the climatic conditions in the Mediterranean Sea are predicted to become largely unsuitable for *C. amentacea*, with a potential risk of extinction in the whole basin under the business-as-usual scenario.

4.4. Interacting multiple stressors

Species responsiveness to climate change will affect and be affected by interactions with various biotic and abiotic factors (Cahill et al., 2014). For example, multiple anthropogenic stressors can amplify the negative effects of climatic stressors and facilitate ecosystem shifts towards alternative states (Strain et al., 2014) that can include urchin barrens, mussels beds and turf algae (Lemée et al., 2012; Connell et al., 2014). Phase-shifts from canopy dominated habitats to barrens have been observed in the Eastern Mediterranean Sea when functionally diverse tropical fishes invaded from the Red Sea (Sala et al., 2011), and these as well as native herbivores are expected to spread with climate change, further threatening *Cystoseira* habitats (Gianni et al., 2017) in addition to the global climate threats reported in this paper. The co-occurrence of multiple biotic and abiotic factors makes it difficult to isolate the effects of climate change alone on the loss of macroalgal forest biodiversity, and climatic niche models do not incorporate the interactive effects of other stressors or variables for which often no simulated data are available. Climatic niche models also do not incorporate evolutionary processes, which could help populations to adapt to changes and colonise new niches (Somero, 2012). A future greater predictive power will need to direct research toward better understanding and modelling the contribution of such factors that are still poorly captured. Despite these limitations, the climatic niche tracking of the different species can still give a confident indication of where and when the greatest impacts are most likely to occur (e.g., Assis et al., 2018), which populations are most crucial to be protected to maintain high genetic diversity and connectivity, and where conservation would be most beneficial, thereby guiding local management efforts to promote climatic resilience (O'Leary et al., 2017). There is growing evidence that the management of multiple local stressors can increase the resilience of canopy algae to climatic factors (Strain et al., 2014). For instance, *Cystoseira* resilience to temperature stress can increase when nutrient loads are decreased (Strain et al., 2015), which could be related to indirect positive effects on the bacterial communities (Mancuso et al., 2016). By determining what habitats provide the greatest resilience in the face of climate change and protecting these from human disturbance, managers may enhance the ability of ecosystems to withstand climatic disturbances (O'Leary et al., 2017).

4.5. Conclusions and future perspectives

The study underlines the importance of complying with the lower emissions objective recently set in the COP21 of the United Nations framework convention on climate change (UNFCCC) and of managing genetic diversity to build up resilience of these key but highly threatened coastal ecosystems. *Cystoseira* canopy-forming macroalgae characterize specific communities (EUNIS A3.132, A3.333 and A3.234) (Davies et al., 2004). In the Mediterranean Sea, they represent the most complex and stable communities that can dominate the shallow euphotic fringe and essentially have no functional equivalent (Benedetti-Cecchi et al., 2001), particularly in wave exposed areas where *C. amentacea* dominates (Bulleri et al., 2002). Their loss would have cascading effects on the whole ecosystem and the services that it provides (Thrush et al., 2011; Araújo et al., 2013). The environmental changes under this objective of climate mitigation would still affect the *Cystoseira* macroalgae distribution, but range shifts would be limited mostly to the Eastern Mediterranean area. On the contrary, the highest emissions scenario (RCP 8.5) would expose coastal ecosystem to profound changes, including extinction risk and genetic erosion in both Mediterranean and North Atlantic ecosystems. COP21 committed to goals of GHG reduction that are ambitious and perhaps hard to achieve (Tomlinson, 2015). However, considering the interplay of global with local stressors, we suggest that acting on reducing and carefully planning the distribution of local pressures should be a priority. This would be a relatively easier and faster solution compared to climate mitigation that could help increase resilience on global stressors and minimize the habitat loss, while allowing more time for the species to adapt, especially in the Mediterranean region.

Declarations of interest

None.

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synergies and TRade-offs for the adaptive management of multiple Impacts in coastal Systems, PRIN 2010-2011, 2010PBMAXP_003, Italian Ministry of Education, University and Research).

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.04.013.

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